

**SENSORY STRUCTURES ON THE OVIPOSITOR OF THE
BALL GALL FLY *EUROSTA SOLIDAGINIS* (FITCH)
(DIPTERA: TEPHRITIDAE)**

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Abstract.—The structural features of the ovipositor, its associated sensilla, and its inversion membrane were investigated by scanning electron microscopy. Anteriorly directed, scale-like outgrowths of the integument arranged in triangular-shaped quadrants cover the inversion membrane. Campaniform and trichoid mechanosensilla are found on the inner valves of the ovipositor while a series of shallow pits containing ampullae-like sensory structures occur on both the dorsal and ventral surfaces of the distal portion of the organ. The ventro-lateral margins near the ovipositor tip have distinct depressions on either side which contain two types of chemosensilla. The number of these chemosensilla is not consistent between specimens. In most cases, there are two sensilla on each side but in some specimens there are two sensilla in the right pit and three in the left. The possible functional role of all these sensilla during oviposition is postulated.

The ball gall fly, *Eurosta solidaginis* (Fitch) is known to oviposit in several species of goldenrod (Felt, 1940). In western New York State, Uhler (1951) demonstrated a distinct preference by the fly for *Solidago canadensis* L. over several species of goldenrod. However, in central Pennsylvania, Greenwald, McCrea and Abrahamson (1984) and Abrahamson, McCrea and Anderson (1989) have shown that *Solidago altissima* L. is the preferred host plant for this fly. Studies conducted by Miller (1959) in the South revealed that when *S. altissima* occurs with *S. gigantea* Ait. and *S. ulmifolia* Muhl., the fly will oviposit on all three.

No hypothesis has been put forth of how *E. solidaginis* can differentiate between goldenrod species for oviposition. Schoonhoven (1983) noted that a number of dipteran species use chemoreceptors on tarsi, labella, and ovipositors in finding suitable host plants for oviposition. The structure and possible functions of chemosensilla, together with mechanosensilla, have been recently reported on the ovipositors of two species of Tephritidae: *Urophora affinis* Frauenfeld (Zacharuk et al., 1986) and *Rhagoletis pomonella* (Walsh) (Stoffolano and Yin, 1987). In this paper, we describe the sensilla present on the ovipositor of another tephritid, *Eurosta solidaginis* and postulate the manner in which they function during egg laying.

MATERIALS AND METHODS

Twelve specimens of *Eurosta solidaginis* initially used in this study were obtained from the insect collections of the State University of New York, College of Arts and Science at Geneseo. These flies had been reared from galls collected locally on *Solidago canadensis*. An additional 12 specimens were obtained from galls on *S. altis-*



Figs. 1-9. 1. Ventral view of ovipositor and inversion membrane $\times 50$. Bar = $67\text{ }\mu\text{m}$. O = ovipositor, formed from fusion of outer valves. Arrow indicates inner valves. S = inversion membrane with scale-like outgrowths of the integument arranged in triangular-shaped quadrants. 2. Enlarged view of scale-like outgrowths of integument on inversion membrane $\times 200$. Bar = $18.7\text{ }\mu\text{m}$. 3. Fusion of valves to form ovipositor $\times 400$. Bar = $8.65\text{ }\mu\text{m}$. Arrows indicate 4 outer valves (ov) of ovipositor iv = inner valve. Note trichoid sensilla on right inner valve. 4. Sensilla on ventral surface of inner valves $\times 400$. Bar = $8.6\text{ }\mu\text{m}$. D = dome-shaped sensilla. T = trichoid sensilla of inner valves. Also note small trichoid sensilla on lateral margin of

*sim*a in February 1988 by Dr. Warren G. Abrahamson of Bucknell University. When received, the galls were placed in rearing cages at room temperature for 10–14 days, at which time the flies emerged. All specimens were air dried for 7–10 days and attached to stubs, gold-coated on a Polaron diode sputterer and examined with an ISI-Alpha-9 Scanning Electron Microscope. The dried specimens gave a clearer picture of components than did fresh material and, thus, critical point drying was not used.

RESULTS

The ovipositor and inversion membrane (Fig. 1) corroborate the description cited by Uhler (1951:9) for the external genital system. He noted the "sharp, pointed, chitinized ovipositor" and that the "ovipositor sheath (i.e., inversion membrane) . . . bears chitinized projections on its surface." These are scale-like outgrowths of the integument and are directed anteriorly. They are arranged in triangular shaped quadrants (Fig. 2). The significance of this scale pattern is not known.

A ventral view of the ovipositor is clearly seen in Figures 1 and 3. Although the valves appear fused, they are not. Specimens softened by boiling in potassium hydroxide reveal a membrane between them and the dorsal part of the ovipositor. Anterior to the point of contact of the inner valves, three small sensilla may be seen on each valve (Fig. 4). The sensilla are evenly spaced and are different with regard to type and arrangement on each valve. The right inner valve contains two campaniform sensilla and one trichoid sensillum, while the left inner valve contains three trichoid sensilla. All the sensilla are directed medially (Fig. 4).

The fusion of the outer valves and cerci forms the pointed ovipositor which Uhler (1951) described. On the outer, lateral margin of the expanded ovipositor near the base, is a small trichoid sensillum (Figs. 6, 7). Three more sensilla are located along the outer lateral margin between the base of the ovipositor and the point of contact of the ventral valves. Comparable structures were not discernable on the dorsal or ventral portions of the valves. However, posteriorly to the point of fusion near the tip of the ovipositor, a number of small ampulloid sensilla may be seen on both the ventral and dorsal surface (Figs. 8, 9). On the ventro-lateral margins near the posterior region, where the ovipositor narrows to form the sharp tip, there are two pits containing chemosensilla. The number of these sensilla was not consistent for all specimens. In most cases, each pit contained two sensilla. However, in three of the 24 specimens we examined, there were two sensilla in the right pit and three in the left (Fig. 9).

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outer valves, just below figure number. 5. Ventral genital opening $\times 400$. Bar = $11.2\ \mu\text{m}$. 6. Trichoid sensillum on outer valve near base. $\times 1,000$. Bar = $4.5\ \mu\text{m}$. 7. Enlarged view of trichoid sensillum on outer valve. $\times 3,000$. Bar = $1.04\ \mu\text{m}$. 8. Dorsal view of posterior portion of ovipositor $\times 700$. Bar = $5.12\ \mu\text{m}$. Note ampulloid sensilla arranged in pairs. 9. Ventral view of apical portion of ovipositor. $\times 1,000$. Bar = $3.46\ \mu\text{m}$. Chemosensilla in pits occupy lateral margins. The usual number of sensilla is two in each pit. However, in three of the 24 specimens examined, there were 3 in one pit and two in the other. Notice difference in shape of sensilla. Ampulloid sensilla are also visible on ventral surface. A = ampulloid sensillum. B = chemosensilla in pits.

DISCUSSION

The structural relationships seen in the ovipositor and inversion membrane of *Eurosta* are quite different from that described from such diverse forms as *Biosteres longicaudatus* (Braconidae), a parasite of the Caribbean fruit fly *Anastrepha* (Greany et al., 1977), the carrot fly *Psila rosae* (Psilidae) and the cabbage root fly *Delia brassicae* (Anthomyiidae) (Behan and Ryan, 1977), the blow fly *Phormia regina* (Calliphoridae) (Wallis, 1962), the sorghum shootfly *Antherigona soccata* (Anthomyiidae) (Ogwaro and Kokwaro, 1981), and the face fly *Musca autumnalis* (Muscidae) (Hooper et al., 1972). The ovipositors of these insects are all segmented structures and contain setal and sensillar patterns that appear to be much more similar to each other than to *Eurosta*. This is because the ovipositor of tephritids is homologous with only segments eight and beyond in the flies mentioned above (Dr. Allen Norrbom, 1986, pers. comm.). While the ovipositor structure is quite different, many of the sensory structures appear similar and are probably functionally similar as well, even though verification must await further experimentation.

Trichoid sensilla have been repeatedly shown to function as mechanoreceptors (Wallis, 1962; Behan and Ryan, 1977; Ogwaro and Kokwaro, 1981; Hooper et al., 1972; Zacharuk et al., 1986; Stoffolano and Yin, 1987). Thus, one can readily postulate that the function of the small trichoid sensilla on the lateral margin of the ventral valve of the ovipositor is to transmit positional information to the fly through deformation of the sensilla as the ovipositor is inserted into the goldenrod tissue. Similarly, the trichoid sensilla on the ventral surface of the two inner valves would be presumed to be mechanoreceptors in the more immediate vicinity of egg release. This would be in agreement with what Stoffolano and Yin (1987) postulated for the trichoid mechanosensilla found on the ovipositor of *Rhagoletis pomonella*.

The two campaniform sensilla on the right inner valve are remarkably similar in appearance to the "dome-shaped" sensilla shown by Greany et al. (1977) at the tip of the ovipositor of *Biosteres longicaudatus*. Similar campaniform sensilla were reported on the ovipositor of *Urophora affinis* by Zacharuk, et al. (1986) and on the oviposition apparatus of *R. pomonella* by Stoffolano and Yin (1987). Greany et al. (1977) also showed TEM micrographs with a definite pore at the tip of the sensillum and concluded it had a chemosensory function—monitoring the chemical environment in the vicinity of oviposition. Schoonhoven (1983) noted that *Anastrepha suspensa* (Loew) (Tephritidae) can measure acidity and the presence of oviposition pheromone in fruit with its ovipositor. Similar assumption can be made for *Eurosta*, with the "dome-shaped" sensilla monitoring the chemical environment in the immediate vicinity where the egg would be released. However, confirmation of this would necessitate TEM studies.

Chemical monitoring of oviposition sites and/or host plant tissues undoubtedly also occurs in the chemosensilla near the tip of the ovipositor. The sensilla in each pit are not all the same. In each pit, the "terminal-most" sensillum is broadly rounded at its tip while the one(s) anterior to it have a slender curved tip with a suggestion of a pore at the bend. Although no specific pore has yet been clearly demonstrated in these particular sensilla, similar structures in other species have been shown to have pores and to have a chemosensory or gustatory function. The differences sometimes in number and shape of these sensilla in their respective pits would indicate, however, that they probably are sensing different chemicals, or the pH, etc. in the

environment of the host plant tissue. Interestingly, the large chemosensilla which Wallis (1962) illustrated on the anal plate of the blow fly *Phormia* are similar to the anteriormost chemosensilla occurring in the pits near the tip of the ovipositor of *Eurosta*. In *Phormia*, these sensilla have a gustatory function, enabling the fly to taste the ovipositional substrate.

The probable function of the small ampullae-like structures which occur on the dorsal and ventral surfaces of the posterior portion of the ovipositor are more difficult to ascertain. There does not appear to be the pore relationship one would expect if they were chemosensory, nor can one detect micro-hair-like structures that might suggest a mechanosensory function. It is possible that they are part of a water-sensing system, but there is no proof for it at this time. What is clear is that there are a sufficient number of different types of sensilla to account for the fly's ability to control oviposition and egg release. It also can account for the times in which *Eurosta* has been known to pierce goldenrod tissue but not release eggs (Uhler, 1951; Abrahamson, pers. comm., 1985).

ACKNOWLEDGMENTS

We thank Dr. Allen Norrbom, Systematics Entomology Laboratory, USDA, and Dr. John Stoffolano, Department of Entomology, University of Massachusetts, and Dr. Robert Beason, Biology Department, SUNY College of Arts and Science, Geneseo, New York, for their advice and suggestions after reading the manuscript. We are also indebted to Dr. Warren C. Abrahamson, Biology Department, Bucknell University, for providing some of the specimens used in this study. The technical assistance of Ms. Elizabeth Netzbund is also greatly appreciated.

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Received July 23, 1986; accepted January 25, 1989.